

A COMPARATIVE BEHAVIORAL STUDY OF THREE GREATER SAGE-GROUSE POPULATIONS

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ABSTRACT.—We compared male strut behavior of the genetically distinct Lyon, Nevada/Mono, California Greater Sage-Grouse (*Centrocercus urophasianus*) population with that of two proximal populations: Nye, Nevada, and Lassen, California. We measured strut rates and nine acoustic components of the strut display in all three populations. Male strut rates did not differ among populations. Acoustic components of the Lyon/Mono and Lassen populations were similar, whereas the Nye population was distinct. The genetically distinct Lyon/Mono population was more similar behaviorally to the Nye population than the genetically similar Nye and Lassen populations were to each other. Overall, the Lyon/Mono population did not exhibit detectable differences in male strut behavior. Reproductive isolation through sexual selection does not appear to have occurred in the Lyon/Mono population. Received 27 September 2004, accepted 19 October 2005.

Two recent studies based on mitochondrial gene sequence (Benedict et al. 2003, Oyler-McCance et al. 2005) and nuclear microsatellite markers (Oyler-McCance et al. 2005) revealed a genetically distinct population of Greater Sage-Grouse (*Centrocercus urophasianus*) on the Nevada/California border (Lyon, Nevada/Mono, California). Those studies indicated that the Lyon/Mono Greater Sage-Grouse population is more genetically distinct from other Greater Sage-Grouse populations than is the newly described (Young et al. 2000) Gunnison Sage-Grouse (*C. minimus*) species. Several factors, including the apparent genetic and geographic isolation of Lyon/Mono sage-grouse from other populations, the degradation and loss of sagebrush (*Artemisia* spp.) habitat, and an overall population decline, have made this a population of interest from both evolutionary and conservation perspectives.

Morphological (Hupp and Braun 1991) and behavioral studies (Young et al. 1994) of Gunnison Sage-Grouse provided evidence that sexual selection had driven speciation in the isolated populations of sage-grouse in southwestern Colorado and southeastern Utah. The use of both mitochondrial (Kahn et al. 1999) and nuclear markers (Oyler-McCance et al.

1999) supported the morphological and behavioral data and led to species designation for the Gunnison Sage-Grouse (American Ornithologists' Union 2000, Young et al. 2000). A similar approach would determine whether the genetic distinctiveness of the Lyon/Mono population has been manifested morphologically and/or behaviorally as it has in Gunnison Sage-Grouse. If so, it could potentially lead to a taxonomic reclassification.

Male mating success and mate-choice cues (Gibson and Bradbury 1985), territoriality (Gibson and Bradbury 1987), components of female choice (Gibson et al. 1991), and male strutting behavior (Young et al. 1994) have been studied previously in the Mono sage-grouse population. However, with the exception of Young et al. (1994), there have been no comparative studies among populations. Young et al. (1994) compared secondary sexual characteristics from male strut displays among three populations—one Gunnison Sage-Grouse population (Gunnison Basin, Colorado) and two Greater Sage-Grouse populations (Mono, California, and Jackson, Colorado). The structure of the Gunnison male strut display was strikingly different from that of the other two populations. However, the comparison of the similarly structured strut display between males from Mono and Jackson indicated statistically significant differences in most of the acoustic measures.

In light of the genetic distinctiveness of Lyon/Mono sage-grouse and the behavioral results of Young et al. (1994), we undertook a further examination of male strut display behavior. We compared the Lyon/Mono popu-

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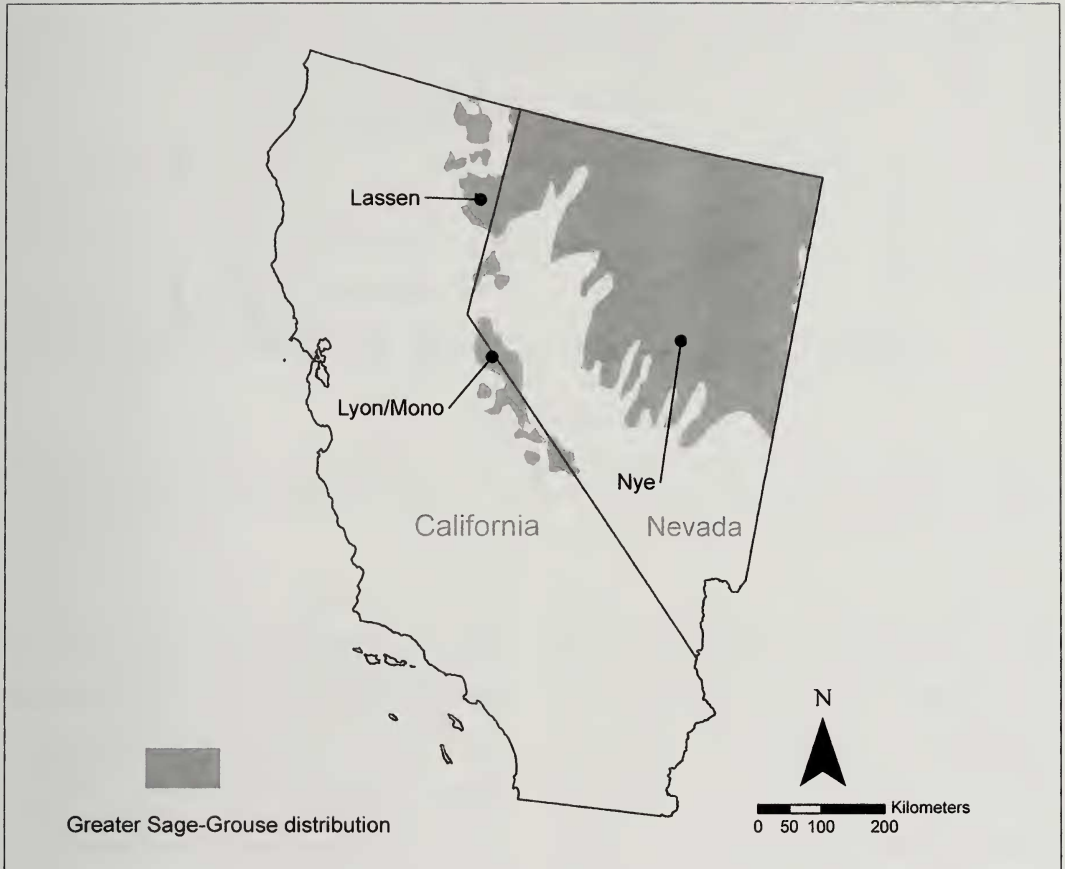


FIG. 1. Current Greater Sage-Grouse distribution in California and Nevada, and locations of three sample populations (modified from Schroeder et al. 2004).

lation with two proximal populations of Greater Sage-Grouse (Fig. 1). We tested the hypothesis that the Lyon/Mono population's behavior is measurably different from that of other Greater Sage-Grouse populations and may, in fact, be considered a separate taxon given the genetic differences. Alternatively, although the Lyon/Mono population appears genetically isolated, behaviorally it may not be significantly different from other Greater Sage-Grouse populations, indicating that sexual selection resulting in pre-mating isolating mechanisms has not occurred.

METHODS

The three populations we studied are from the southwestern edge of the Greater Sage-Grouse range in Nevada and California (Fig. 1). Behavioral measurements of male strut

displays were taken at five leks. Greater Sage-Grouse in Lyon County, Nevada, and Mono County, California, form a connected, interbreeding population (Lyon/Mono). Recordings were completed between 9 and 17 April 2001 at three leks from the Lyon/Mono population: Lyon County, Nevada (Desert Creek 2 lek; $38^{\circ} 42' N$, $119^{\circ} 18' W$; 1,603 m), southern Mono County, California (Long Valley 1 lek; $37^{\circ} 42' N$, $118^{\circ} 48' W$; 2,124 m), and northern Mono County, California (Biedeman lek; $38^{\circ} 12' N$, $119^{\circ} 6' W$; 2,447 m). Of the three recorded Lyon/Mono leks, the Desert Creek and Biedeman leks are farthest apart (123 km). Lassen County, California (Eastside lek; $40^{\circ} 18' N$, $120^{\circ} 0' W$; 1,490 m), is approximately 250 km north and Nye County, Nevada (Roadside lek; $38^{\circ} 42' N$, $116^{\circ} 47' W$; 2,121 m), is approximately 215 km east of the

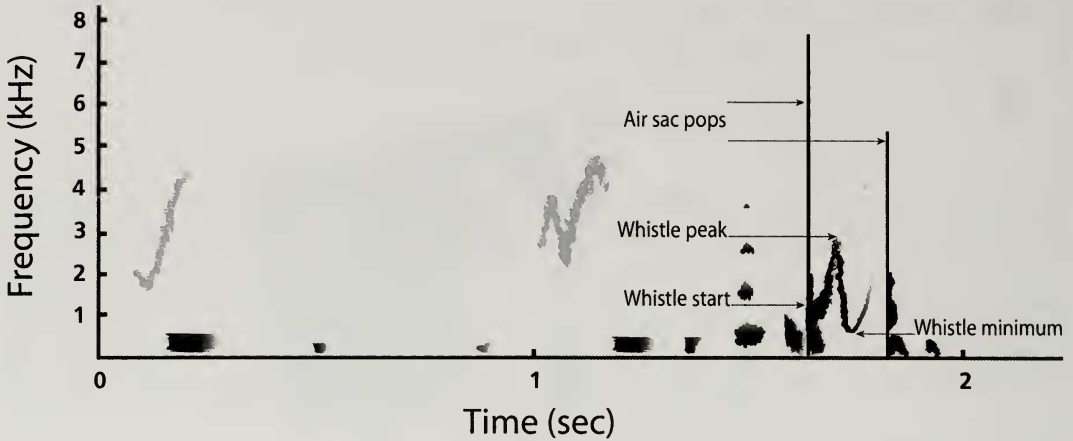


FIG. 2. Typical sonogram of a Greater Sage-Grouse male strut display. The two air sac pops, whistle start frequency, whistle peak, and whistle minimum are labeled. See Table 1 for all acoustic components (modified from Young et al. 1994).

Lyon/Mono population; recordings at these sites were completed between 3 and 11 April 2002. The number of males sampled from each of the five leks was as follows: Desert Creek 2 ($n = 6$), Long Valley 1 ($n = 9$), Biedeman ($n = 9$), Eastside ($n = 11$), and Roadside ($n = 14$); therefore, the sample size for the Lyon/Mono population was $n = 24$.

Males perform a ritualized strut display in which they take a few steps forward and brush their wings twice against their esophageal pouch producing loud swishing noises (Fig. 2). Following these wing movements, males compress air sacs and produce syringeal sounds to complete a single strut display (Hjorth 1970). Male strut displays were recorded and compared using the methods of Young et al. (1994) with the following modifications. Only adult males were monitored, and these were distinguished from juveniles in the field by the presence of a clear white upper breast on adults. Individual males were identified by their tail patterns (Wiley 1973). At least 15 struts per male were recorded using a Sony DCR TRV720 digital camcorder and a Sennheiser MKH70-P48 microphone. Sounds of individual struts were digitized at 22 kHz using Canary 1.2.4 sound analysis software (Cornell Laboratory of Ornithology, Ithaca, New York).

We measured nine acoustic components (Table 1, Fig. 2) and calculated population means derived from individual male averages

for each component. An estimate of repeatability ($[r = s^2_A / (s^2 + s^2_A)]$; Lessells and Boag 1987) was used to measure the proportion of within-individual variation within populations for each component. Repeatabilities range from 0 (low) to 1.0 (high). High repeatabilities indicate that the measured trait varies little within individuals relative to the population variation, suggesting that the trait could respond to sexual selection.

To calculate strut display rate, we timed between-strut intervals using Etholog 2.2, an ethological transcription tool (Ottoni 2000). The display rate for each male was based on 7–40 consecutive struts in which no more than 30 sec had lapsed between struts. Females were present on all leks during strut-rate measurements, but any male included in the strut-rate analyses had to have females within 20 m of them during recording. This criterion lowered the sample sizes (number of males) for population strut-rate estimation (Fig. 3). At the Lassen and Lyon leks, measurements were taken as one female moved throughout the leks. The southern Mono, northern Mono, and Nye leks all had multiple females visiting leks over the various days that measurements were taken.

We used analysis of variance (ANOVA) to assess differences among populations for each acoustic component and strut rate. We then used the GT2-method (Hochberg 1974) to make unplanned comparisons among popula-

TABLE 1. Nine measured acoustic components of male Greater Sage-Grouse strut display in three populations from Nevada and California. Males were recorded while strutting during spring 2001 and 2002.

| Measured variable | Acoustic component | Lyon, Nevada/Mono, California (<i>n</i> = 24) | | Lassen, California (<i>n</i> = 11) | | Nye, Nevada (<i>n</i> = 14) | | <i>P</i> ^a |
|--|--------------------|--|-------|-------------------------------------|-------|------------------------------|-------|-----------------------|
| | | Mean | SE | Mean | SE | Mean | SE | |
| First pop to whistle peak (msec) | 1 | 73.41 | 0.37 | 73.85 | 0.65 | 70.30 | 0.52 | <0.001 |
| Whistle peak to whistle minimum (msec) | 2 | 40.21 | 0.28 | 39.81 | 0.32 | 41.69 | 0.61 | 0.012 |
| Pop to pop (msec) | 3 | 199.89 | 0.73 | 199.64 | 0.97 | 192.24 | 0.88 | <0.001 |
| Whistle start frequency (Hz) | 4 | 861.17 | 7.61 | 861.65 | 10.97 | 930.19 | 20.19 | <0.001 |
| Whistle peak (Hz) | 5 | 2,619.83 | 21.06 | 2,657.32 | 23.09 | 2,873.84 | 42.85 | <0.001 |
| Whistle minimum (Hz) | 6 | 533.58 | 5.89 | 514.48 | 7.56 | 637.26 | 9.63 | <0.001 |
| Whistle start to peak difference (Hz) | 7 | 1,771.61 | 20.69 | 1,795.22 | 23.94 | 1,944.72 | 35.09 | <0.001 |
| Whistle peak to minimum difference (Hz) | 8 | 2,096.48 | 21.90 | 2,151.64 | 17.61 | 2,241.51 | 39.14 | 0.002 |
| Whistle start to minimum difference (Hz) | 9 | 333.90 | 11.33 | 353.70 | 13.99 | 290.38 | 16.80 | 0.020 |

^a ANOVA.

tion means with unequal sample sizes for acoustic components. This method uses the studentized maximum modulus distribution *m* to compute a minimum significant difference (MSD). The significance level for the ANOVA was set at $P = 0.05$ and for the GT2-method it was lowered from $P = 0.05$ to $P = 0.017$ using a Bonferroni correction ($\alpha'' = \alpha/k$; Sokal and Rohlf 1995) for multiple tests. We used $\alpha'' = 0.01$ when referring to the studentized maximum modulus *m* critical values table (GT2-method).

RESULTS

All nine acoustic components of the strut display differed among populations (ANOVA,

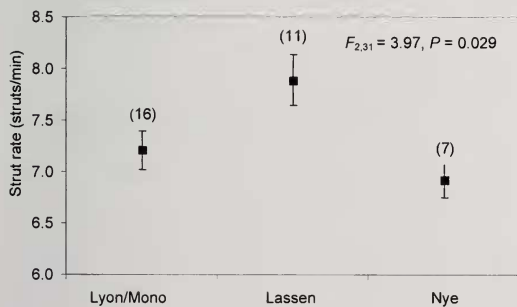


FIG. 3. Means (with standard error bars) and ANOVA result for strut rates of male Greater Sage-Grouse from three populations: Lyon, Nevada/Mono, California; Lassen, California; and Nye, Nevada. Sample sizes (number of males) are in parentheses.

all $P < 0.05$; Table 1). The acoustic components of the males' displays were similar between Lyon/Mono and Lassen, whereas those of Nye males' displays were consistently distinct from those of the other two populations. Nye differed from both Lyon/Mono and Lassen for acoustic components 1 and 3–7 (GT2-test, all $P < 0.01$). For component 8, Nye differed only from Lyon/Mono (GT2-test, $P < 0.010$). All other pairwise population comparisons for minimum significant differences were not significant (GT2-test, all $P > 0.01$).

Repeatability estimates of the acoustic components ranged from 0.41 to 0.84 in Lassen, 0.57 to 0.96 in Nye, and 0.35 to 0.91 in Lyon/Mono (Table 2). The highest repeatability estimate for all three populations was for whistle peak (component 5).

Strut rates (struts/min) differed ($F_{2,31} = 3.97$, $P = 0.029$) among populations (Fig. 3). However, pairwise comparisons between populations indicated that none were significant (GT2-test, all $P > 0.01$). Lassen males had the highest strutting rate (7.84 struts/min), whereas males from Nye had the lowest strutting rate (6.92 struts/min). Lyon/Mono males had an intermediate strutting rate (7.21 struts/min).

DISCUSSION

We measured behavioral traits and secondary sexual characteristics that are related to sexual selection in sage-grouse, which could

TABLE 2. Repeatability estimates of strut display acoustic components within individual males from three Greater Sage-Grouse populations in California and Nevada. Males were recorded while strutting during spring 2001 and 2002.

| Acoustic component | Lyon, Nevada/ Mono, California <i>n</i> = 24 | Lassen, California <i>n</i> = 11 | Nye, Nevada <i>n</i> = 14 |
|--------------------|--|--|------------------------------|
| 1 | 0.51 | 0.78 | 0.65 |
| 2 | 0.35 | 0.44 | 0.62 |
| 3 | 0.64 | 0.74 | 0.65 |
| 4 | 0.57 | 0.67 | 0.79 |
| 5 | 0.91 | 0.84 | 0.96 |
| 6 | 0.57 | 0.68 | 0.79 |
| 7 | 0.53 | 0.80 | 0.88 |
| 8 | 0.74 | 0.49 | 0.87 |
| 9 | 0.41 | 0.41 | 0.57 |

therefore lead to divergence. Based on behavioral differences in male strut displays, our study did not support the idea that the genetically distinct Lyon/Mono population should be considered for separate taxonomic status. The Lyon/Mono and Lassen populations were similar to each other, while the Nye population was the most unique across nine acoustic components of male mating displays. However, across six components (1–4, 6, 9), the Nye versus Lassen populations were either more different or as different as Nye versus Lyon/Mono populations (Table 1). Even though the Lyon/Mono population is genetically distinct, male mating behaviors are more similar to those of the Nye population than those of the genetically similar Nye and Lassen populations are to each other (Table 1).

The repeatability estimates generally varied widely across populations. However, three acoustic components (3, 5, and 9) were relatively comparable among the three populations. The high repeatability estimates for components 3 (pop to pop) and 5 (whistle peak) indicate that these traits vary little within individual males relative to the variation within populations and could potentially respond to selection. Young et al. (1994) also found high repeatability estimates for whistle peak, which has been shown to be related to female mate choice (Gibson and Bradbury 1985, but see Gibson et al. 1991). A low repeatability for component 9 (whistle start to minimum difference) is most likely the result of high levels of variability within individuals

rather than a lack of genetic variation or inaccuracies in measurement (Boake 1989). Nye had the highest repeatability estimates for seven of the nine acoustic components, suggesting low variation in the acoustic measurements, despite samples being taken across several days with multiple females being present.

Although strut rates did differ among populations, pairwise comparisons of strut rate did not differ statistically between populations. This result agrees with the observations of Young et al. (1994), who found that strut rates did not differ between two Greater Sage-Grouse populations—Mono, California, and Jackson, Colorado. Strut rates may vary with time of day, time of season, and proximity of females (R. M. Gibson pers. comm.); therefore, variation in strut rate within and between males may outweigh differences in strut rates among populations except in strong cases of population divergence.

Our results suggest that the Lyon/Mono population does not exhibit any appreciable behavioral differences in male mating displays from other Greater Sage-Grouse populations. The Lyon/Mono population is significantly different genetically from the Lassen population (Benedict et al. 2003, Oyler-McCance et al. 2005), yet behaviorally, the Lyon/Mono and Lassen populations have similar acoustic strut components and strut rates. The implications of the slight behavioral differences observed in the Nye population on female mate choice may be determined upon further behavioral observations that include additional leks, years, and populations. It is possible that there are measurable differences in acoustic components of the strut display between most populations, but these differences are generally minimized by gene flow.

The Lyon/Mono population is genetically more diverse and distinct than the Gunnison Sage-Grouse species (Kahn et al. 1999, Oyler-McCance et al. 1999, Benedict et al. 2003, Oyler-McCance et al. 2005). Using mitochondrial DNA sequence, Benedict et al. (2003) estimated that the Lyon/Mono population has been isolated from other Greater Sage-Grouse populations for tens of thousands of years. Yet, neither local adaptation to ecological or environmental factors, nor genetic drift, nor sexual selection has led to detectable pheno-

typic (behavioral) differences in this population. Reproductive isolation does not appear to have occurred through sexual selection in the Lyon/Mono population as it has in the Gunnison Sage-Grouse species.

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